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Research Article

Eutrophication boosts the competitive advantage of invasive gibel carp over endangered crucian carp

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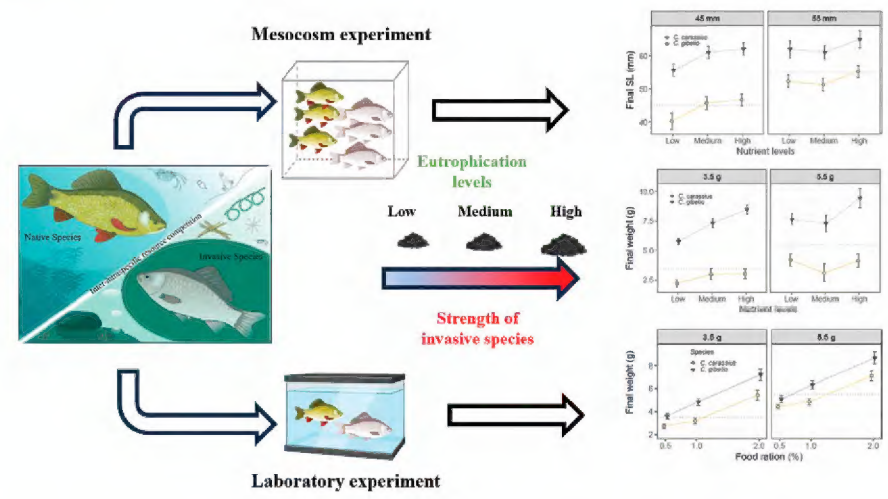
Abstract

Anthropogenic eutrophication poses a significant threat to freshwater environments globally. It also influences the population dynamics of invasive and native species, yet the cumulative effects of eutrophication and invasive species on native organisms are not well understood. We used invasive gibel carp (*Carassius gibelio* Bloch, 1782) and native crucian carp (*Carassius carassius* Linnaeus, 1758) as model taxa to investigate how eutrophication influences their interspecific competition. *Carassius carassius* is being outcompeted by invasive *C. gibelio* across most of its native range, and eutrophication may play a role in the competitive displacement of *C. carassius*. We explored how varying eutrophication levels influence growth and survival of both species in laboratory and mesocosm experiments, where we exposed them to different feeding rations and nutrient levels, respectively. We hypothesized that (1) *C. gibelio* benefits more from increased nutrient levels than *C. carassius*—which favors invasive *C. gibelio* over native *C. carassius* in interspecific competition—and that (2) the growth and survival of *C. carassius* deteriorate under interspecific competition with *C. gibelio* compared to intraspecific competition. Our experiments revealed that excess nutrient availability was more beneficial to the invasive *C. gibelio*. Overall, *C. gibelio* individuals grew more than *C. carassius*, and the difference between the two species increased with nutrient levels in both experiments, especially in the weight of smaller individuals. Moreover, interspecific competition led to lower survival in *C. carassius* but not in *C. gibelio* in the mesocosm experiment. This study shows that eutrophication may modulate interspecific competition, and cultural eutrophication of freshwater habitats may enhance the success of invasive species.

Graphical abstract



Key words: Biodiversity loss, growth rates, interspecific competition, invasive species, nutrient enrichment, survival

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Introduction

Anthropogenic eutrophication, which can occur over time frames as short as a decade, affects most of the world's freshwater ecosystems (Smith and Schindler 2009; El-Sheekh et al. 2021). Runoff from urban and agricultural areas carries nutrients, sediment, and industrial effluents that accelerate eutrophication beyond natural levels and trigger changes to natural ecosystems (Smith et al. 1999; Prepas and Charette 2003; Smith 2003; European Environment Agency 2018).

Eutrophication enriches freshwaters with nutrients, particularly phosphorus and nitrogen, which promote the growth of aquatic organisms (Schindler 2006; Khan and Mohammad 2014). High nutrient levels promote rapid algal growth, which can outcompete macrophytes in the littoral zone or lead to harmful algal blooms (Vadeboncoeur et al. 2021). Eutrophication-driven shifts from macrophyte-based to algae-based production may also trigger changes in important ecosystem functions, such as the loss of refuge habitats for macrozoobenthos provided by macrophytes (Kolar and Boukal 2020; Kolar et al. 2023) and a reduction in food sources for fish and other predators that rely on macrozoobenthos (Smith 2003; Šmejkal et al. 2023).

The effects of eutrophication on fish competition can vary depending on the taxa, degree of eutrophication, and other environmental factors (Smith 2003; Gaygusuz et al. 2007; Wang et al. 2009; Khan and Mohammad 2014). Nutrient-rich conditions can favor certain species, while those adapted to low-nutrient conditions can be outcompeted by species that thrive in nutrient-rich environments (Tilman 1982; Smith 2003). For example, eutrophication significantly impacted fish communities in a reservoir on the Dnipro River, Ukraine (Bondarev et al. 2023): the number of fish species and total biomass increased with increasing eutrophication levels. Another study conducted in the San Francisco Bay Area of California, USA, found that elevated nutrient concentrations supported approximately five times higher biomass of the invasive mosquitofish (*Gambusia affinis* Baird & Girard, 1853) than low nutrient concentrations (Preston et al. 2018). These studies demonstrate that eutrophication alters fish community dynamics by species numbers and biomass, thereby promoting the dominance of certain invasive species.

The nutrient-driven hypothesis states that nutrient availability can significantly influence community composition, species interactions, and ecological dynamics (Seehausen et al. 1997; Milardi et al. 2022). Nutrient loading determines species composition of natural communities (Vašek et al. 2016), and eutrophication can lead to diversity loss and dominance of invasive species (Milardi et al. 2018). Moreover, a recent modeling study showed that species invasions in simple food webs most often succeed in warm, eutrophic habitats (Dijoux et al. 2024). The effect of nutrient availability on individual taxa depends on their characteristics, such as resource needs, resource use efficiency, and trophic position (González et al. 2010). Many invasive freshwater species tend to have fast life histories and thus high resource demand (Blumenthal 2006; González et al. 2010; Tibbets et al. 2010). These species thrive in nutrient-rich environments and tolerate low dissolved oxygen levels (Kauppi et al. 2017; Preston et al. 2018). For example, *Pterygoplichthys* fishes (Günther, 1864) are likely to benefit from eutrophication due to an abundant supply of food, which facilitates their colonization (Davis et al. 2000). Similarly, studies on *Cyprinus carpio*

(Linnaeus, 1758) in North America and Western Europe have shown that the ample availability of food resources has significantly aided its colonization and spread (Copp et al. 2005; Taylor et al. 2014; Souza et al. 2022).

Invasive species can also be better adapted to exploit available food resources with a wider dietary range than native species, and hence may have higher growth rates under optimal feeding conditions (Mooney and Cleland 2001; Tapkir et al. 2022, 2023). This may create opportunities for invasive species to fill less utilized ecological niches, thereby changing the composition and functioning of the ecosystem (Lekevičius 2009). For example, invasive species from the family Cyprinidae, such as *Cyprinus carpio* and *Hypophthalmichthys molitrix* (Valenciennes, 1844), can also feed on plants and hence grow and reproduce more quickly than native fish species that cannot utilize plants as a food source (Gozlan et al. 2010). Moreover, species like *Cyprinus carpio* and *Carassius gibelio* (Bloch, 1782) actively disturb sediments and increase sediment resuspension, further promoting eutrophication of a given water body (Meller and Crowl 2006; Tarkan et al. 2012a; Vilizzi et al. 2015).

The native crucian carp (*Carassius carassius* Linnaeus, 1758), once widespread and common in northern and central Eurasia, is now classified as endangered in many European countries due to competition with *C. gibelio* (Kottelat and Freyhof 2007; Jeffries et al. 2016; Šmejkal et al. 2024, 2025), raising concerns about the potential loss of this native species (Sayer et al. 2011, 2020; Tapkir et al. 2022; Auwerx and Wichelen 2023; Thomas et al. 2024). On the other hand, *C. gibelio*, a globally successful invasive fish species, has increased its distribution range at the expense of *C. carassius* (Šmejkal et al. 2024). The presence of *C. gibelio* alters plankton communities, enhances planktonic algal growth, and prevents the development of submerged macrophytes and large-bodied zooplankton, thereby exacerbating eutrophication (Richardson et al. 1995; Razlutskij et al. 2021). *Carassius gibelio* initially had a wide natural distribution range, extending from East Asia to Central Europe (Copp et al. 2005; Aydin et al. 2011; Wouters et al. 2012). It became invasive in Europe due to the accidental introduction of the eastern lineage in the 1940s and 1950s to Eastern Europe (Hensel 1971; Šmejkal et al. 2024). Since then, it has proliferated across most of the continent (Rylková et al. 2013; Ribeiro et al. 2015), and it has also entered North America (Alberta province, Canada) (Elgin et al. 2014; Pentyliuk et al. 2023). However, the role of eutrophication in its success in interspecific fish competition is poorly understood, despite the fact that this occurred largely in EU countries heavily affected by eutrophication (Directive 1992; Penning et al. 2008).

Thus, this study aims to investigate the competitive interactions between *C. gibelio* and *C. carassius* and to address knowledge gaps concerning the impact of eutrophication on the individual growth and survival of both invasive *C. gibelio* and native *C. carassius* in order to clarify how eutrophication influences the competitive interactions between these two omnivorous fish species. We specifically focused on phosphorus-driven eutrophication, as phosphorus availability is an important factor for the classification of cultural eutrophication in freshwaters (Rosset et al. 2014). By conducting both laboratory and mesocosm experiments, we manipulated nutrient availability while keeping fish density constant, allowing us to measure potential differences in growth rates and survival under varying eutrophic conditions. We hypothesized that (1) the addition of nutrients would disproportionately benefit *C. gibelio*, thereby exacerbating its competitive advantage

over *C. carassius* and negatively affecting the growth of the native species, and (2) the growth and survival of *C. carassius* would decline under interspecific competition with *C. gibelio* compared to intraspecific competition.

Materials and methods

Fish, zooplankton, and macrophyte collection and maintenance

Fish were collected at two locations in Czechia, which contained either just *C. carassius* or both native and invasive *Carassius* species (*C. carassius*: Ujezdec pond, 49.8991464N, 14.9512814E; *C. gibelio*: Vrábče, 49.5444106N, 14.6012644E). Fish were maintained in the laboratory in glass tanks (64 × 60 × 34 cm) filled with 130 L of clean, oxygenated water for 1 week at 20 °C under a 12L:12D photoperiod. Fish were fed daily with 1% of their body weight in commercial feed (C-3 Carpe F, Skretting, Stavanger, Norway). Fish species were identified according to their morphological characters (Szczerbowski 2002; Kottelat and Freyhof 2007). The main identification characters were the serration of the last unbranched spine of the dorsal fin, gill raker count, and the shape of the head and fins.

To provide conditions similar to natural habitats in the mesocosm experiment, we collected zooplankton, phytoplankton, and macrophytes (*Limnophila aquatica* and *Ceratophyllum demersum*) in water bodies near Vrábče and in the Motovidlo fishpond near České Budějovice (48°92.5521'N, 14°37.5078'E and 48°59.9982'N, 14°22.9186'E). They were kept separately in 500 L outdoor circular vats before being used in the mesocosm experiment. Macrophytes were soaked in sugar water (1 kg/100 L) overnight to remove other organisms (snails, oligochaetes, etc.) and then transferred to clean water for rinsing.

Laboratory experiment

The experiment ran for 84 days from May 20 to August 12, 2022. It was conducted in 18 glass aquaria (64 × 60 × 34 cm), each filled with 130 L of clean, oxygenated water in the laboratory at the Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czechia. The aquaria were equipped with an aerator and maintained under a 12L:12D photoperiod. Each aquarium received 10 fish (5 individuals of each species; a total of 90 *C. carassius* and 90 *C. gibelio*). Total initial biomass in each aquarium was kept as close to 40 g as possible (mean ± SD = 42.6 ± 3.3 g), although some aquaria deviated from this value (min–max range = 37.7–52.8 g) due to the size of available fish. Initial *C. carassius* standard lengths were 48.3 ± 7.1 mm, 46.3 ± 6.7 mm, and 47.7 ± 7.6 mm in the low, medium, and high feed treatments, respectively, while lengths of *C. gibelio* were 50.7 ± 2.9 mm, 49.3 ± 2.0 mm, and 50.3 ± 2.2 mm in the low, medium, and high feed treatments, respectively.

Individual fish length and weight were recorded every 14 days throughout the experiment. Fish identity in aquaria was established by clipping. Aquaria were divided into three groups based on daily food supplementation, calculated as 0.5%, 1%, or 2% of total fish biomass in each aquarium, quantified every 14 days from repeated measurements of all individuals. At the end of the experiment, all surviving fish were measured; *C. carassius* were released back to their source site, while invasive *C. gibelio* were overdosed with MS-222.

Mesocosm experiment

The mesocosm experiment ran for 104 days from June 8 to September 20, 2022. It was conducted in 24 outdoor mesocosms at the Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czechia. Each tank (UV-resistant high-density polyethylene, 98 cm length × 91 cm height × 90 cm width) received 800 L of aged tap water and 7.5 kg of washed river sand (grain size 1–4 mm; SP Bohemia, k.s., České Budějovice). Four weeks before the introduction of fish, macrophytes (wet weight 100 g each of *L. aquatica* and *C. demersum*) and 2 L of a well-mixed phytoplankton and zooplankton inoculum were added to each tank. Tanks were randomly divided into three nutrient-level groups based on the amount of added feed pellets (C-3 Carpe F, Skretting, Stavanger, Norway; low: 0 g, medium: 25 g, high: 50 g). The mesocosms were then allowed to stabilize and release nutrients from the pellets.

The manipulated factors included fish assemblage composition (intraspecific vs. interspecific) and nutrient levels (low, medium, and high). The intraspecific treatment (three replicates per nutrient level) received 10 individuals of *C. carassius* per tank, while the interspecific treatment received 5 *C. carassius* and 5 *C. gibelio* per tank (five replicates per nutrient level), i.e., a total of 165 *C. carassius* and 75 *C. gibelio* were used in this experiment. Fish identity was established by clipping. The intraspecific treatment of *C. gibelio* was not included due to the study's main focus on the impact of invasive *C. gibelio* on native *C. carassius* and the limited number of tanks.

Initial total fish biomass in each tank was kept as close to 40 g as possible (mean ± SD [min–max range], intraspecific treatment: 41.2 ± 0.9 g [40.2–43.0 g]; interspecific treatment: total = 39.8 ± 1.8 g [36.4–42.7 g], *C. carassius* = 20.3 ± 1.2 g [17.6–22.3 g], *C. gibelio* = 19.5 ± 0.8 g [18.1–21.1 g]). Initial *C. carassius* standard lengths were 49.6 ± 5.4 mm, 49.7 ± 5.7 mm, and 50.9 ± 4.7 mm in the low, medium, and high experimental treatments and 51.2 ± 4.2 mm, 52.4 ± 4.1 mm, and 47.2 ± 3.9 mm in the control treatment, respectively. Initial *C. gibelio* standard lengths were 48.2 ± 2.9 mm, 49.5 ± 3.7 mm, and 48.7 ± 2.3 mm in the low, medium, and high nutrient treatments, respectively.

At the end of the experiment, the length of each surviving fish was measured to the nearest 0.1 mm and weighed to the nearest 0.1 g (SI-132-3 scales; Excell, New Taipei City, Taiwan). *C. carassius* were released back to their source site, while invasive *C. gibelio* were overdosed with MS-222. Water parameters and zooplankton density were measured at 5-week intervals on four sampling dates during the experiment. Conductivity ($\mu S \cdot cm^{-1}$) was measured with a WTW Multi 3430 multimeter (WTW, a Xylem brand, Weilheim, Germany). Chlorophyll-*a* (relative fluorescence units, RFU) was measured with a YSI Pro DSS multimeter (YSI, a Xylem brand, Yellow Springs, USA). Water transparency (cm) was measured with a Sneller tube (Kolar et al. 2021). Zooplankton was sampled with a tube sampler (diameter 7 cm, length 100 cm) equipped with a one-way valve at the bottom. Four whole-column samples were collected from four regularly spaced locations within each mesocosm to reduce the effects of plankton patchiness and pooled in a 10 L bucket. After mixing, a 3 L subsample was collected and filtered through a 250 μm zooplankton net. Filtered zooplankton was collected in 50 ml vials and preserved with 4% formaldehyde for subsequent counting and identification. Additionally, six data loggers (HOBO Pendant Temperature/Light 64 K Data Logger,

Onset Computer Corporation, Bourne, Massachusetts, USA) were placed in the middle of the water column in six random mesocosms to continuously monitor water temperature during the experiment (mean ± SD = 19.5 ± 0.5 °C).

For total phosphorus (TP) determination, water samples were taken from all tanks at four sampling dates: the beginning (day 1), two intermediate measurements, and day 104 at the end of the experiment. Samples were filtered through a 40 µm polyamide sieve to remove zooplankton and/or other coarse particles, followed by acid digestion. TP concentration was then measured using the semi-micro modification method (Kopáček and Hejzlar 1993). We did not measure total nitrogen (TN) because our specific aim was to investigate the direct effects of phosphorus-driven eutrophication on competitive interactions between species, as phosphorus availability is a key limiting factor in many aquatic ecosystems (Sterner and Elser 2003).

Data analyses

Laboratory and mesocosm experiment: initial conditions and fish survival and growth

We used one-way ANOVA for the laboratory experiment and two-way ANOVA for the mesocosm experiment to test whether the total initial fish biomasses, TW_{ini} (g), differed between treatments (Suppl. material 1). To test the effects of syntopy, nutrient levels, and their interaction on the proportion of surviving individuals in the mesocosm experiment, we used a generalized linear model (GLM) with a logit link function and a quasibinomial error distribution to account for overdispersion in the data.

Final size could only be measured in surviving individuals, i.e., we quantified growth conditional on survival. Individual growth trajectories in body length (SL, mm) and wet weight (W, g) of both species in the laboratory experiment were consistent with linear rather than exponential growth or shrinkage (details not shown). We therefore considered only the initial and final measurements of body size—SL_{ini}, SL_{fin}, W_{ini}, and W_{fin}—in the laboratory experiment and expressed individual growth increments (mm.day^{-1}, g.day^{-1}) in both experiments as $(SL_{fin} - SL_{ini})/D$ and $(W_{fin} - W_{ini})/D$, with D = 84 days for the laboratory experiment and D = 104 days for the mesocosm experiment.

Because the initial size of the fish could not be fully standardized (see above) and preliminary inspection of the data indicated possible size-dependent growth in both experiments, we always used initial size as a predictor of final size:

$$SL_{fin} = a + b\ SL_{ini} \quad (1)$$

$$W_{fin} = c + d\ W_{ini} \quad (2)$$

Slope estimates of b = 1 and d = 1 in Eqs. (1) and (2) represent size increments that do not vary with initial size. Values of $b < 1$ and $d < 1$ correspond to growth that slows during ontogeny, and values of $b > 1$ and $d > 1$ indicate accelerating growth in larger individuals that could occur, for example, due to asymmetric, size-based competition between fish in the same aquarium or tank.

We used linear mixed models to test the effects of experimental treatments on fish growth in both experiments. We assumed species-specific growth patterns and always considered that the intercepts and slopes in Eqs. (1) and (2) differ between

species. We did not have a *priori* hypotheses on the possible effects of food concentration on size-dependent growth of both species in both experiments or on the effect of syntopy treatment on size-dependent growth in *C. carassius* in the mesocosm experiment. We therefore did not test the effects of initial size, species identity, and experimental treatments on growth using a single model. Instead, we used a model selection approach and compared several models corresponding to different assumptions on the effects of species identity and experimental treatment on fish growth in both experiments (Suppl. material 1: tables S1, S2).

We accounted for possible density dependence of individual growth by including total initial biomass, TW_{ini}, as an additional predictor in all models of the laboratory data, and the proportion of surviving fish, *DD* (irrespective of species), as an additional predictor in all models of the mesocosm data (see Suppl. material 1 for details). Finally, we included aquarium or tank identity as a random intercept in each model to account for the nested structure of the data, i.e., measurements of multiple individuals of both species from each aquarium or tank (Zuur et al. 2009). We verified that this random structure was appropriate for the data (see Suppl. material 1 for details).

For the mesocosm data, we analyzed separately (i) the effect of species identity only in the interspecific treatment, mirroring the laboratory experiment, and (ii) the effect of syntopy treatment only on *C. carassius*. This allowed us to keep a limited number of models in each analysis and directly address our main questions about the effects of eutrophication on the competitive interactions between both species. The model sets included six models for the laboratory experiment and the first analysis of the mesocosm experiment and eight models for the second analysis of the mesocosm experiment (Suppl. material 1: tables S1, S2). Some of these models had heteroskedastic residuals; in such cases, we assumed species- or nutrient level-specific residual variance. We used the corrected Akaike information criterion (AICc) to identify the best (i.e., most parsimonious) model with the lowest AICc and other plausible models (ΔAICc $\leq$ 2) for each dataset and response (Burnham and Anderson 2002).

Mesocosm experiment: environmental data

Temporal changes in environmental parameters (chlorophyll-*a*, conductivity, and water transparency) and zooplankton density (determined to the taxonomic level of Copepoda and Cladocera) were initially tested using a Principal Response Curve (PRC) analysis (Van den Brink and Ter Braak 1999). However, the PRC did not detect any significant temporal treatment effects on zooplankton composition (pseudo-F = 0.4, P = 0.807), likely due to high initial variability among replicates and limited statistical power. We therefore used Redundancy Analysis (RDA) to capture temporal trends in the mesocosm experiment. Sampling day and its interaction with the treatments were used as categorical explanatory variables, while the environmental variables and zooplankton density served as response variables. All explanatory variables in both analyses were centered.

We then used generalized linear mixed models (GLMMs) with a Gamma distribution and log-link function to test the effects of the experimental treatments on TP concentrations, which were not included in the RDA analysis as they were measured only at a subset of dates. Preliminary inspection of the data showed that TP concentrations on Day 0 (when fish were introduced)

differed between treatments and that subsequent temporal changes in TP concentrations were not monotonic. We therefore always included nutrient level as an explanatory variable and used a third-order time polynomial to capture temporal dynamics (equivalent to treating time as a factor). Time was z-scaled (mean = 0, SD = 1) to improve model convergence and interpretability. We used a model selection approach and compared all possible effects of syntopy and nutrient level treatments on TP concentrations at Day 0 and on subsequent temporal changes, as we did not have *a priori* hypotheses on their combined effects on TP dynamics. This yielded 15 models, all incorporating a random intercept for mesocosm identity to account for repeated measures. We used AICc, as for the growth data, to identify the best model.

All univariate analyses were conducted in R version 4.3.3 (R Core Team 2024). We used the packages *glmmTMB* (Brooks et al. 2017) and *bbmle* (Bolker 2023) to fit and compare the GLMs, LMMs, and GLMMs from both experiments, and the package *sjplot* (Lüdecke et al. 2020) to report model parameters. Model residuals were inspected in the package *DHARMa* (Hartig 2020) to verify that they did not violate model assumptions. The best models were illustrated using the package *ggeffects* package (Lüdecke 2018). Instead of post hoc significance tests, we deemed differences between levels of discrete explanatory variables to be "significant" if the respective 95% confidence intervals based on fixed effects did not overlap, and continuous explanatory variables to be "significant" if the 95% confidence interval of the estimate based on fixed effects did not overlap zero. Multivariate analyses were conducted in CANOCO 5 (ter Braak and Smilauer 2012). Statistical significance of the RDAs was assessed using Monte Carlo permutation tests (999 unrestricted permutations under a reduced model).

Results

Laboratory experiment: fish survival and growth

All individuals of both fish species survived in the laboratory experiment. Length- and weight-based growth increments of *C. carassius* were mostly negative in the 0.5% food ration treatment (mean ± SD = -0.24 ± 2.69 mm.month^{-1} and -0.46 ± 0.63 g.month^{-1}), near zero in the 1% food ration treatment (1.03 ± 3.60 mm.month^{-1} and -0.22 ± 0.63 g.month^{-1}), and positive only in the 2% food ration treatment (1.14 ± 2.60 mm.month^{-1} and 0.33 ± 0.59 g.month^{-1}). This contrasted with higher growth increments of *C. gibelio*, which were around zero only in the 0.5% food ration treatment (0.27 ± 2.46 mm.month^{-1} and -0.07 ± 0.30 g.month^{-1}) and almost always positive in the 1% food ration treatment (2.09 ± 3.19 mm.month^{-1} and 0.35 ± 0.60 g.month^{-1}) and in the 2% food ration treatment (3.07 ± 2.94 mm.month^{-1} and 1.43 ± 0.69 g.month^{-1}).

Model selection identified two plausible models for length-based growth and three plausible models for weight-based growth. Food ration affected growth according to all five of these models. Four models also included species-specific dependence of growth on food ration, with an overall steeper response to increased food levels in *C. gibelio* than in *C. carassius* (Fig. 1, Suppl. material 1: tables S1, S3, S4).

The length-based growth was size independent in *C. carassius* (95% confidence intervals of the size slope estimate always overlapped with $b = 1$ in both

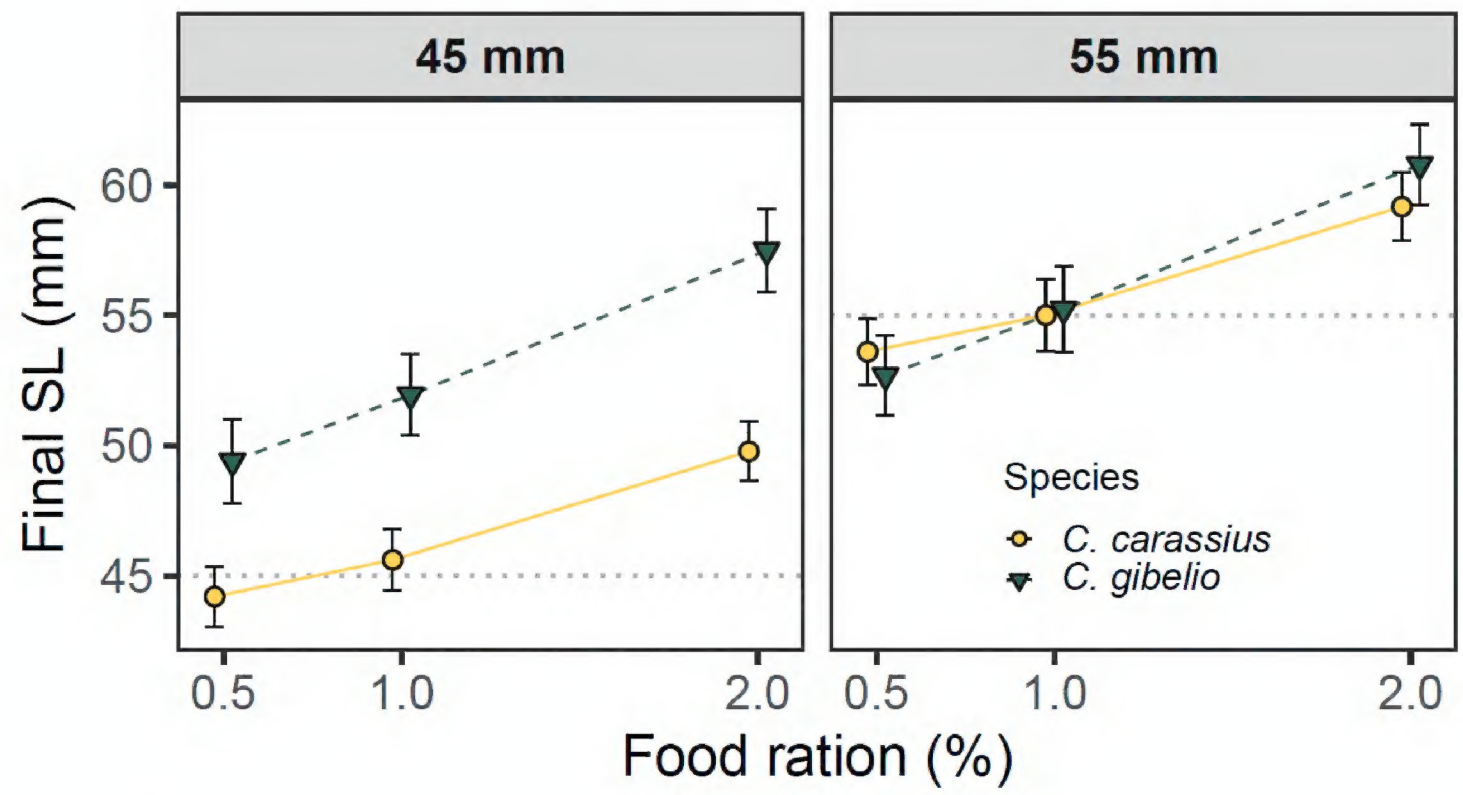

Figure 1. Predictions of length-based (top row) and weight-based (bottom row) growth of *C. carassius* and *C. gibelio* in the laboratory experiment, based on the best model. Predictions are illustrated for two initial sizes (standard length and weight) given in panel headings. Symbols = mean estimates for each species; error bars = 95% confidence intervals based on fixed effects. Total initial biomass adjusted at TW_{ini} = 42.6 g. SL = standard length. The dotted horizontal line in each panel corresponds to zero growth.

plausible models), while initially larger *C. gibelio* individuals grew less in length (b < 1; Suppl. material 1: fig. S1, table S3). That is, within each food ration treatment, *C. gibelio* reached a significantly larger final length than same-sized *C. carassius* only when their initial length was below ca. 50 mm, while individuals of both species above that size (i.e., the largest individuals of *C. gibelio* used in the experiment) reached a similar final size (top row in Fig. 1, Suppl. material 1: fig. S1). At each food ration level, weight-based growth declined with initial body size in both species (95% confidence intervals of the size slope estimate d were always < 1), and *C. gibelio* always reached a larger weight than same-sized *C. carassius* according to the best model (Fig. 1, Suppl. material 1: fig. S1). Finally, we detected a tendency towards positive, rather than negative, density-dependent growth in length of both species (mean estimates: +0.14 mm per 1 g increase in initial biomass, Suppl. material 1: table S3), but the growth in weight was density independent (mean estimates: -0.01 g per 1 g increase in initial biomass, Suppl. material 1: table S4).

Mesocosm experiment: fish survival and growth

The proportion *DD* of surviving fish ranged widely between 0.3 and 1.0 (mean ± SD: 0.85 ± 0.20) in individual tanks, and survival differed markedly between both species. While only two out of 75 *C. gibelio* died, 34 out of 165 *C. carassius* individuals did not survive until the end of the experiment. The quasibinomial GLM model revealed no statistically significant effects of syntopy ($\chi^2(1) = 4.59$, $P = 0.27$), nutrient levels ($\chi^2(2) = 13.64$, $P = 0.17$), or their interaction ($\chi^2(2) = 0.58$, $p = 0.93$) on *C. carassius* survival. We did not test the effect of experimental treatments on *C. gibelio* survival.

Growth increments of *C. carassius* were near zero in the intraspecific treatment (0.14 ± 1.43 mm.month^{-1} and -0.01 ± 0.34 g.month^{-1}) and mostly negative in the interspecific treatment (mean ± SD across all three nutrient levels: -0.25 ± 1.17 mm.month^{-1} and -0.28 ± 0.24 g.month^{-1}), while the growth increments of *C. gibelio* in the interspecific treatment (3.39 ± 1.33 mm.month^{-1} and 0.99 ± 0.42 g.month^{-1}) were always positive except for one large individual in the medium nutrient level treatment. In each nutrient level treatment, *C. gibelio* reached larger final sizes than *C. carassius* of the same initial size (Suppl. material 1: figs S2, S3).

Model selection identified only one plausible model for both length- and weight-based growth data constrained to the interspecific treatment (Suppl. material 1: table S2). While *C. gibelio* of the two sizes illustrated in Fig. 2 was always predicted to grow (i.e., the entire 95% confidence interval of the final size was above the initial size), *C. carassius* of the same sizes was predicted to significantly shrink or not grow (i.e., the entire 95% confidence interval was below or overlapped the initial size). According to these models, both species also responded differently in length and weight growth to increasing nutrient level treatments and initial body size. The differences in predicted final lengths of both species were constant across all three nutrient levels and decreased with initial length (Fig. 2, upper row) due to the significantly shallower slope *b* in *C. gibelio* than in *C. carassius* (Suppl. material 1: table S5). On the other hand, differences in the predicted final weights of *C. carassius* and *C. gibelio* did not change with initial weight due to the almost equal slopes *d* in both species (Suppl. material 1: table S6), but the differences in predictions increased from the low to high nutrient level treatment (Fig. 2, bottom row). We found no evidence for density-dependent growth in length or weight in the data constrained to the interspecific treatment (Suppl. material 1: fig. S2, tables S5, S6).

With the data constrained to *C. carassius* in both syntopy treatments, three models were plausible for each measure of growth (Suppl. material 1: table S2). The best models predicted that the growth of *C. carassius* in length or weight did not vary significantly between nutrient levels within each syntopy treatment, i.e., the 95% confidence intervals of the final size overlapped between treatments (Fig. 3, Suppl. material 1: fig. S3). Moreover, syntopy had a significant effect on the growth of *C. carassius* in weight but only a limited effect on their growth in length. Individuals of the same initial weight were always predicted to reach significantly larger final weights in the intraspecific than in the interspecific treatment, and the predicted difference was the same for all initial sizes and nutrient treatments (Fig. 3, Suppl. material 1: fig. S3, bottom row). However, the effect of syntopy on length-based growth was more subtle: while individuals with $SL_{ini} = 45$ mm were always predicted to grow significantly in the intraspecific treatment, their growth in the interspecific treatment was never significantly different from zero irrespective of the nutrient

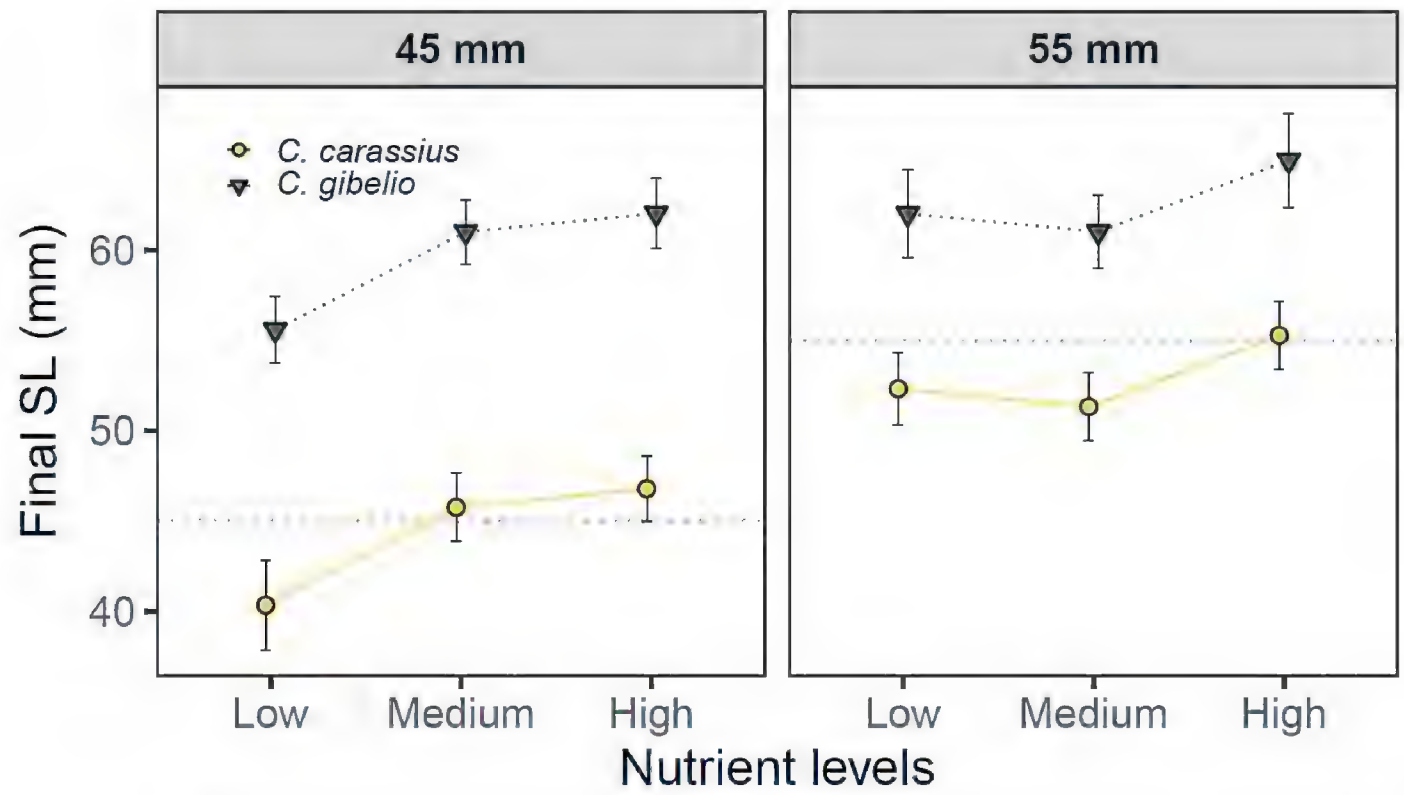

Figure 2. Predictions of length-based (top row) and weight-based (bottom row) growth of *C. carassius* and *C. gibelio* in the interspecific treatment in the mesocosm experiment, based on the best model. Predictions are illustrated for two initial sizes (standard length and weight) given in panel headings. Symbols = mean estimates for each species; error bars = 95% confidence intervals based on fixed effects. Total initial biomass adjusted at TW_{ini} = 42.6 g. SL = standard length. The dotted horizontal line in each panel corresponds to zero growth.

level. This difference disappeared for larger individuals (SL_{ini} = 55 mm) due to the shallower size slope estimate *b* in the intraspecific treatment; these individuals were predicted to significantly shrink in length in the low and medium nutrient level treatments and remain at the initial length in the high nutrient level treatment (Fig. 3 Suppl. material 1: fig. S3, upper row). Finally, the best models identified no trend in final length and a tendency towards larger final weight of surviving fish in tanks with a lower proportion of survivors (Suppl. material 1: fig. S3, tables S5, S6).

Mesocosm experiment: environmental responses

Total phosphorus (TP) concentrations were higher in the medium (mean ± SD = 62.2 ± 32.6 $\mu g.L^{-1}$) and, especially, high nutrient level treatments (101.7 ± 110.1 $\mu g.L^{-1}$) than in the low nutrient level treatment (61.5 ± 41.6. $\mu g.L^{-1}$) at the start of the experiment, with no clear differences between fish identity treatments until Day 68 (Suppl. material 1: fig. S4). Over time, TP concentrations

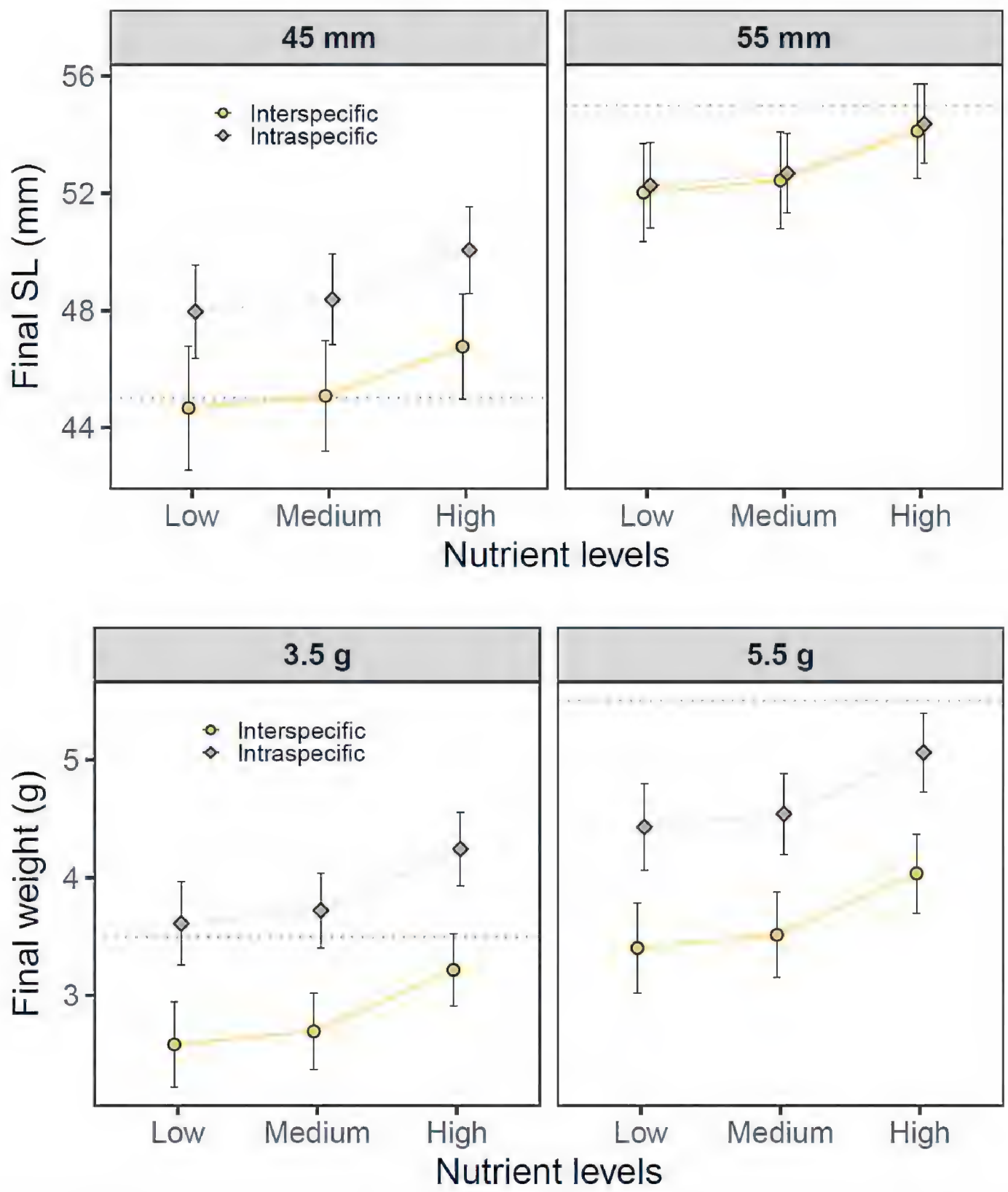

Figure 3. Predictions of length-based (top row) and weight-based (bottom row) growth of *C. carassius* in the intraspecific and interspecific treatment in the mesocosm experiment, based on the best model. Predictions are illustrated for two initial sizes (standard length and weight) given in panel headings. Symbols = mean estimates for each treatment; error bars = 95% confidence intervals based on fixed effects. SL = standard length. Proportion of surviving individuals adjusted at *DD* = 0.9. The dotted horizontal line in each panel corresponds to zero growth.

declined in the interspecific treatment, most notably in the high nutrient level treatment, while they remained relatively stable in the intraspecific treatment, particularly under low nutrient conditions (Suppl. material 1: fig. S4). On Day 68, TP concentrations were higher in the intraspecific than in the interspecific treatment at each nutrient level. Thereafter TP remained stable in most treatments but increased slightly in the intraspecific, low-nutrient-level treatment. The final TP concentrations were similar across all nutrient levels but were higher in the interspecific (mean ± SD = 62.3 ± 1.6 $\mu g.L^{-1}$) than in the intraspecific treatment (35.8 ± 7.9 $\mu g.L^{-1}$). These values were close to the initial values in the low nutrient level treatment (Suppl. material 1: fig. S4). Model selection identified two plausible models describing TP concentrations (Suppl. material 1: tables S7, S8), which revealed treatment-specific temporal changes of TP concentrations in the mesocosm experiment.

Water transparency, conductivity, and chlorophyll-*a* concentration also changed significantly over time, with differences observed between treatments (RDA: pseudo-F = 31.2, P = 0.001, explained variation = 88.62%, Fig. 4a, Suppl. material 1: table S9).

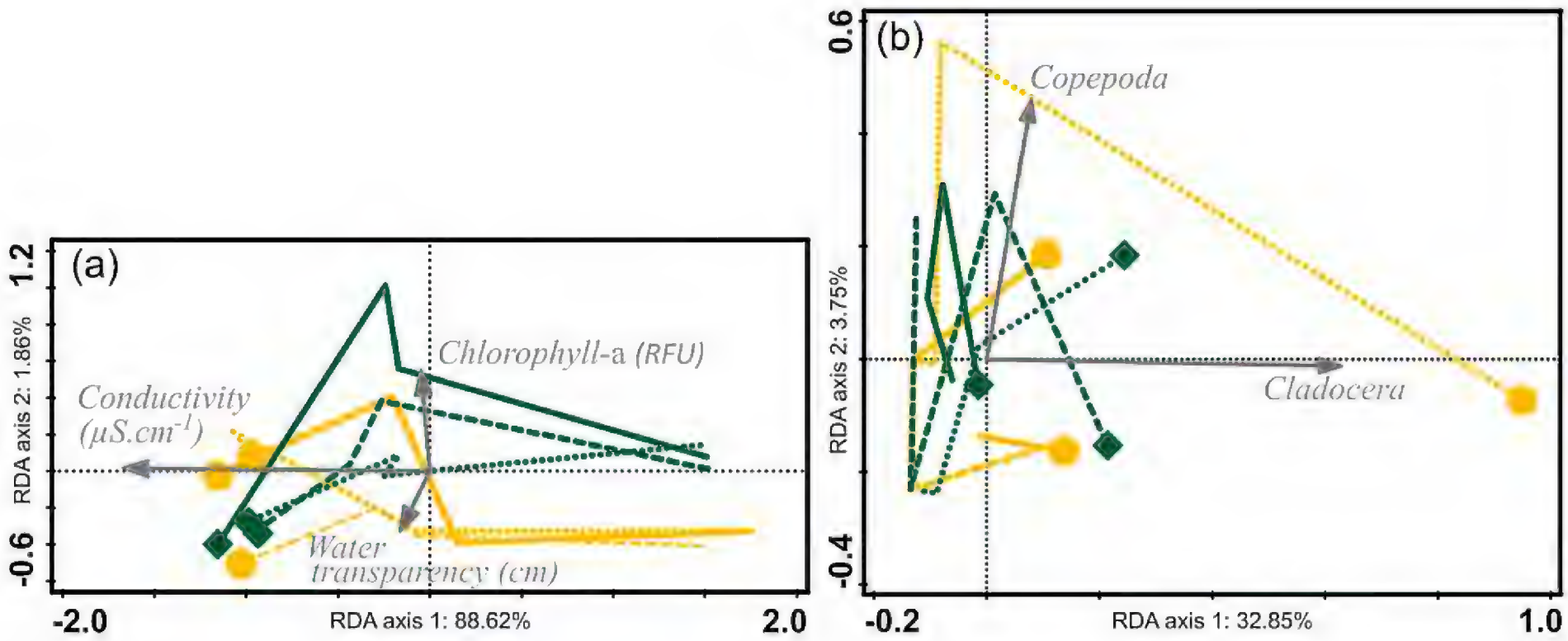

Figure 4. Redundancy analyses (RDA) diagrams showing interaction between time and treatments in the mesocosm experiment for **a**. Water transparency, conductivity, and chlorophyll-*a* and **b**. Zooplankton community composition (Cladocera and Copepoda). Yellow circles and lines = intraspecific treatments (with only *C. carassius*), green diamonds and lines = interspecific treatments (with *C. carassius* and *C. gibelio*), dotted lines = low nutrient treatment, dashed lines = medium nutrient treatment, and solid lines = high nutrient treatments. Symbols indicate the start of the experiment.

The first RDA axis was associated with conductivity, which showed higher values at the start of the experiment in all treatments. Initially, the mesocosms displayed similar environmental conditions, but both treatments, especially fish identity, influenced chlorophyll-*a* (mainly along the second axis) and water transparency (along both the second and third axes), while water conductivity decreased over time similarly across all mesocosms (Fig. 4a). At the end of the experiment, water transparency was slightly higher and chlorophyll-*a* concentrations were lower in mesocosms with intraspecific *C. carassius* treatments compared to interspecific treatments.

Finally, zooplankton densities and the ratio between Cladocera and Copepoda also changed over time with differences between treatments (RDA: pseudo-F = 1.8, P = 0.019, explained variation = 32.85%, Fig. 4b, Suppl. material 1: table S10), although no clear patterns separating the treatments could be identified due to high initial random variability between replicates. Cladocerans, which showed a gradient along the first RDA axis, initially dominated the zooplankton community, especially in mesocosms with low nutrient levels, but then rapidly declined irrespective of the nutrient levels. Copepods showed a gradient along the second RDA axis but did not show clear temporal trends. By the end of the experiment, zooplankton had nearly disappeared from the mesocosms irrespective of the treatment.

Discussion

Eutrophication and invasive fish are widespread drivers of ecological change in freshwater ecosystems (Stendera et al. 2012; Gallardo et al. 2016; Busst and Britton 2017; Carosi et al. 2023). We hypothesized that the benefits of added nutrients and increased food availability would be greater for the invasive *C. gibelio* than for the native *C. carassius*, in line with the nutrient-driven hypothesis. Overall, our data supported this hypothesis: growth rates of *C. gibelio* increased more with nutrient addition than those of *C. carassius* in both mesocosm and laboratory experiments. These findings indicate that *C. gibelio* may benefit from increased nutrient availability more than the native *C. carassius*.

Evidence for nutrient-driven hypothesis

Our experimental results show that invasive *C. gibelio* grows comparatively faster than native *C. carassius* under nutrient-rich conditions, demonstrating the ability of the invasive species to better exploit nutrient-enriched environments. Invasive species with lower trophic positions and broad diets can thrive in nutrient-rich environments, often at the expense of native species (Gido and Franssen 2007). Invasive *C. gibelio* has been shown to grow faster than *C. carassius* in natural water bodies as well as in mesocosms (Tapkir et al. 2022), and eutrophication may further boost *C. gibelio*'s competitive abilities.

When invasive species are competitively superior to native species in exploiting resources, the likelihood of coexistence decreases, often leading to the invasive species dominating native species (Leger and Espeland 2010). Exploitative competition between *C. gibelio* and *C. carassius* led to a significant weight reduction and increased mortality of *C. carassius* in the mesocosm experiment. This phenomenon is likely a contributing factor to the local disappearance of *C. carassius* populations (Šmejkal et al. 2024). Furthermore, understanding how different levels of eutrophication affect *C. carassius* and its ability to coexist with invasive *Carassius* species can guide *C. carassius* conservation efforts (Navodaru et al. 2002; Tarkan et al. 2016).

Effects of intra- and interspecific competition

In our mesocosm experiment, weight increments of *C. carassius* were higher under intraspecific rather than interspecific competition, suggesting that *C. carassius* may acquire or allocate more resources toward growth when competing with conspecifics rather than heterospecifics (Fuller 2016). This could be due to differences in intra- and interspecific competitive interactions—in particular, *C. gibelio* is the stronger competitor, leading to fewer per capita resources for *C. carassius* in the interspecific treatment. In established relationships between species, intraspecific competition is usually more intense, as individuals compete directly for identical resources, potentially driving individuals to invest more in growth to outcompete peers (Gurevitch et al. 1992; Adler et al. 2018). In contrast, interspecific competition is usually less direct since species often occupy different ecological niches, leading to resource partitioning and reduced direct competition (Simberloff 2005; Adler et al. 2018; Eurich et al. 2018). Because the interaction between invasive and native *Carassius* species is relatively new, it appears that native *C. carassius* struggles in interspecific competition, as its weight-based growth increments were always lower in the interspecific than in the intraspecific treatment in our mesocosm experiment. When comparing different nutrient-level treatments in syntopy, *C. gibelio* showed a stronger growth response to increased food availability than *C. carassius*, which aligns with the nutrient-driven hypothesis.

When matched for size, *C. carassius* always had lower weight increments compared to *C. gibelio*, indicating that *C. gibelio* dominated resource utilization when both species co-occurred. Similarly, initial body size and food availability determined the growth rates of *C. gibelio* and *C. carassius* in the laboratory experiment, and the results were qualitatively identical and quantitatively similar to the patterns observed in the mesocosm experiment. All else being equal, *C. carassius* had a lower growth rate than *C. gibelio*, suggesting a species-specific intake rate or food conversion efficiency of the pellets used in the experiment. Finally, the slower growth of larger individuals of both species can be attributed to size-related differences in

metabolic rate and energy allocation, since larger individuals may require more energy to maintain their body size, leaving less energy available for growth (Tsoumani et al. 2006; Dmitriew 2011). Growth rate strongly depends on food intake (Jobling and Baardvik 1994) and typically declines in larger individuals in most fish species unless they undergo an ontogenetic diet shift (Ohlberger 2013).

Results from the laboratory experiment should be interpreted with caution, as food accessibility in aquaria is high and competing species have limited opportunities for niche partitioning under such conditions. Both study species have flexible life-history characteristics and can adapt their growth and reproductive investment to current biotic interactions in a given water body (Brönmark and Miner 1992; Holopainen et al. 1997; Emiroğlu et al. 2012). Thus, it may be useful to study their competition under different biotic interactions, such as with varying piscivorous species (de Meo et al. 2023). Future studies incorporating a broader body size range of invasive and native species, representing more natural interactions with multiple age cohorts, could address this issue. Furthermore, varying biomass of the invasive species from the initial to the final phase of invasion could help clarify the mechanisms behind competitive exclusion between the two *Carassius* species. Finally, an experimental setup with higher structural complexity and larger tanks could also provide better insight into competition.

The mesocosm experiment highlights the significant role of nutrient levels and fish identity in shaping aquatic ecosystem dynamics. Total phosphorus (TP) was initially higher in medium- and high-nutrient treatments, but it declined rapidly in high-nutrient conditions and remained relatively stable in low-nutrient treatments, leading to similar TP levels across treatments by the end of the experiment. Species composition affected chlorophyll-*a* and transparency, with intraspecific treatments showing higher transparency and lower chlorophyll-*a*. Zooplankton, initially dominated by cladocerans, declined over time and eventually disappeared, highlighting how nutrient inputs and species interactions shape long-term nutrient cycling and ecosystem function.

Nutrient availability as a driver of invasion success

Elevated nutrients can provide a favorable environment for the rapid establishment of species inocula, leading to an increased impact of invasion (Byers 2002; González et al. 2010; Gallardo et al. 2016; Preston et al. 2018). Increased nutrient levels, particularly phosphorus and nitrogen, promote rapid growth of phytoplankton and subsequent algal blooms (Smith and Schindler 2009; Dodds and Smith 2016; Rolton et al. 2022). Therefore, eutrophication stimulates primary productivity and enhances the growth of algae and/or submerged macrophytes, leading to easily accessible resources for invasive species with a broad dietary range (David et al. 2017).

Increased nutrient input likely promotes higher fish biomass through increased food availability (Lancaster and Drenner 1990), which can provide a competitive advantage to invasive species over native species (Havel et al. 2015; Fernández-Alías et al. 2022). In the present mesocosm and laboratory study, nutrient-rich conditions and higher food intake appeared to favor the invasive *C. gibelio* and played a significant role in its interspecific competition with *C. carassius*. We conclude that invasive *C. gibelio* grew faster than *C. carassius* because it benefited from additional plant-based food resources promoted by eutrophication. Previous studies have also shown that *C. gibelio* exhibits superior resource utilization efficiency compared to native *C. carassius*, resulting in faster growth rates (Tapkir et al. 2022, 2023), which is consistent with our nutrient manipulation experiments.

Eutrophication also changes the physicochemical characteristics of water bodies, which may favor invasive species that thrive in nutrient-rich environments (Alexander et al. 2017). Recent studies have shown that *C. gibelio* tends to exploit underused food resources by occupying a lower trophic niche, leading to a competitive advantage over native *C. carassius* (Özdilek and Jones 2014; Tapkir et al. 2023) by capitalizing on the abundance of easily accessible primary producers. Our study further suggests that chlorophyll-*a* concentrations were higher and water transparency lower when both *C. gibelio* and *C. carassius* were present compared to mesocosms with only *C. carassius*. Taken together, this indicates that invasive *C. gibelio* can contribute to the feedback loop of eutrophication, in which increased nutrient availability promotes algal growth and provides more food to *C. gibelio* (Crivelli 1995; Tarkan et al. 2012b), whose presence further aggravates eutrophication symptoms.

Europe has been invaded by several entities from the *Carassius auratus* complex, including various mitochondrial lineages associated with the taxa *C. auratus*, *C. gibelio*, and *C. langsdorfii* (Wouters et al. 2012; Kalous et al. 2013; Gu et al. 2022), as well as cytotypes exhibiting different ploidy levels. It is not possible to distinguish these entities without genetic analysis. As they may possess distinct biological characteristics, including gill raker counts (Hensel 1971; Papoušek et al. 2008; Tesfaye et al. 2025), their growth responses to eutrophication may differ accordingly.

Conclusion

This study provides novel insights into the role of multiple anthropogenic stressors that can act synergistically to negatively affect biodiversity (Šmejkal et al. 2025). Eutrophication, in combination with the effective utilization of resources by invasive species, facilitates the competitive advantage of invasive *C. gibelio* over native *C. carassius*. By employing a combined mesocosm and laboratory approach, we demonstrated that nutrient and food enrichment not only enhance the growth and survival of *C. gibelio* but also exacerbate growth rate differences between *C. carassius* and invasive *C. gibelio*. We used a substitution design (Inouye 2001) in both experiments due to the limited number of replicates. Future studies using a response surface design along a larger gradient of fish densities (Inouye 2001) could help elucidate the importance of intra- and interspecific competition between *C. carassius* and *C. gibelio* for the long-term dynamics of their distribution in Europe.

Future research can focus on determining whether cultural eutrophication generally favors the success of invasive species in aquatic ecosystems, as in the case of two competing species of the genus *Carassius*. The implications of these synergistic effects are significant for freshwater biodiversity conservation and invasive species management. These findings highlight the need for stricter nutrient management policies to mitigate eutrophication in freshwater habitats, thereby reducing ecological pressure on vulnerable native species such as *C. carassius*. Future work should also examine the role of other environmental stressors, such as climate change and habitat fragmentation, in mediating interspecific interactions between invasive and native species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

The field sampling and experimental protocols used in this study were performed under the guidelines and permission of the Experimental Animal Welfare Commission under the Ministry of Environment of the Czech Republic (ref. no. CZ 01679). Fish were kept under the permission of the Ministry of Agriculture (ref. no. 4253/2019-MZE-17214).

Use of AI

No use of AI was reported.

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Author contributions

S.T., K.T., Y.S., and M.Š. participated in experimental work; M.Š., D.B., V.K., and C.D. designed the study; S.T., M.Š., L.K., K.T., and Y.S. prepared the data for analysis; M.Š., S.T., D.B., V.K., and C.D. conducted the data analysis; and S.T., M.Š., and D.B. wrote the first draft. M.Š., D.B., V.K., L.K., and C.D. edited the manuscript. All authors contributed substantial feedback during manuscript preparation.

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Data availability

Data will be made available on the authors' ResearchGate profile upon publication of this paper.

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Supplementary material 1

Additional images and tables

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